http://www.urbanfischer.de/journals/saeugetier



Physical and population parameters of Eurasian badgers (Meles meles L.) from Mediterranean Spain

By E. REVILLA, M. DELIBES, A. TRAVAINI, and F. PALOMARES

Department of Applied Biology, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Sevilla, Spain

> Reiceipt of Ms. 20. 10. 1998 Acceptance of Ms. 05. 05. 1999

Abstract

Biometry, reproduction, and density of the Eurasian badger (*Meles meles*) population living in the Doñana area, Mediterranean Spain, were investigated. These badgers were smaller, lighter, and less sexually dimorphic than those from any other region of this widely distributed species. There was no significant seasonal variation in body mass. Most of the births occurred in January. Reproduction occurred once a year in 67% of the territories. All females older than two years had bred at least once; and 65% bred in the calendar year of capture. Badger densities ranged from 0.23 to 0.67 individuals/km². These densities are between five and 125 times lower than that of populations inhabiting temperate ecosystems, where badgers feed on earthworms. Biometric and reproductive parameters of this population fit into the clinal variation found across Europe, where badgers are smaller and breed earlier to the south. Low densities can be explained as a functional response to the low productivity of Mediterranean areas and can also be expected for many other parts of the species' distribution area, where earthworms are not the staple food.

Key words: Meles meles, biometry, density, reproduction, Mediterranean areas

Introduction

Mediterranean environments are in some ways different from those found in Eurasian temperate landscapes. Differences include physical environmental characteristics (temperature, humidity), type and structure of vegetation (evergreen sclerophyllous scrubland), prey availability (abundant beetles, reptiles, and rabbits), and strong seasonal patterns (mild winters which are considered the 'good' seasons, and extremely dry and hot summers which are the 'bad' ones; DI CASTRI and MOONEY 1973; DELIBES 1975). Badgers inhabiting the Iberian Peninsula have been described as Meles meles marianensis Graells, 1897, however the only feature used in the description of this subspecies was the paler colour on back and flanks (LONG and KILLINGLEY 1983). Nowadays no validation of this taxon exists, or knowledge about differences with other badger populations (Long and KILLINGLEY 1983). The IUCN conservation status of badgers in Spain is insufficiently known (BLANCO and GONZALEZ 1992), as in other Mediterranean countries (GRIFFITHS and THOMAS 1997). GRIFFITHS and THOMAS (1997) remarked on the importance of undertaking research on Mediterranean badgers for the future conservation of the species. In order to improve the scarce knowledge about Mediterranean badgers, we studied biometry, reproduction, and density of animals living in a Mediterranean area of Spain.

Material and methods

Study area and animals

Animals came from an area of about 1000 km², in the SW corner of the Iberian Peninsula (~37°N, 6°30'W). Part of this area is protected by Doñana National and Natural Parks. It has a Mediterranean climate with Atlantic influence (mild wet winters and hot dry summers). Vegetation inside the protected areas is dominated by natural Mediterranean scrubland (*Halimium* spp., *Cistus* spp., *Pistacia lentiscus, Rosmarinus officinalis*), degraded cork oak woods (*Quercus suber*), marshland, sand dunes, and pine plantations (*Pinus pinea*); and by pine and eucalyptus (*Eucalyptus* spp.) plantations elsewhere.

We distinguished between three badger age classes: cubs – those with milk teeth or changing to permanent (until 16 weeks old); yearlings – between 16 weeks and two years (24 months old), and adults – two years or older (NEAL and CHEESEMAN 1996). The first two age classes were determined by body size and tooth characteristics (milk teeth, or newly emerged permanent teeth). Adults and some yearlings (those with permanent teeth) were determined by counts of cementum annuli in pre-molars (KLEVEZAL 1996). This last technique proved accurate in our study area, not only with marked badgers of known age, but also with other carnivore species (ZAPATA et al. 1995, 1997).

Biometry

Between 1983 and 1998 we measured a total of 78 individual badgers, which were live trapped (N = 75) or found dead (N = 3). Trapped animals were permanently marked with a tattoo or with a microchip. In case of recaptures, we used only the measurements recorded at first. The following data were taken: body weight (BW, precision 100 g); head-body length (HB), from the tip of the snout to the dorsal edge of the perineum; tail length (TL), from the dorsal edge of the perineum to the tip of the tail, excluding fur; hindfoot length (HF), from the edge of the calcaneus to the tip of the third phalange; ear length (EL), from the base of the tragus to the tip of the pinna, excluding hair; and hilt (HI), from the top of the shoulder-blade to the end of the foreleg, excluding hand. Lengths were in mm and measured on the left side of the animal. We used only adult animals in the analysis, and excluded also the weight of pregnant females. Variations in body weight between sex classes and seasons were analysed in relation to sex, using a multivariate analysis of variance (MANOVA). Normality and equality of variances were assessed through Kolmogorov-Smirnov and Levene tests (ZAR 1996). Sexual dimorphism was also evaluated using the index male measurement/female measurement (Moors 1980; TRAVAINI and DELIBES 1995).

Reproduction

Data on reproduction were obtained from live trapped and dead animals, and from the monitoring of radiotagged individuals (see Density). Birth dates were estimated (to the nearest month) based on teeth eruption patterns of cubs; by the state of pregnancy following NEAL and CHEESEMAN (1996); and by behavioural changes in radiotagged females, for whom cub presence was later confirmed. We considered that a female had bred if she was pregnant or lactating, or if she had black placental scars in the uterus (PAGE et al. 1994; WOODROFFE 1995; WOODROFFE and MACDONALD 1995 a, b). Females with extended teats were considered to have bred previously. In males we distinguished individuals with abdominal testes from those with descended testes (WOODROFFE and MACDONALD 1995 a; WOODROFFE et al. 1997).

Density

Radio-tracking was the only accurate way of estimating density, since the difficulties in trapping badgers (about 450 night-traps for capturing a single animal, REVILLA 1998) did not allow the use of capture–re-capture techniques. We estimated density in two different populations in the Doñana area.

8

271

Animals from the population in the Coto del Rey zone preyed mainly on rabbit kittens (FEDRIANI et al. 1998; REVILLA 1998), while in the Reserva Biologica zone, the population had no staple food (MARTIN et al. 1995; REVILLA 1998). Between 1994 and 1997 we radio-tagged 17 animals in Coto del Rey, from five territories, and in 1997 we marked three females, from three territories in the Reserva Biologica. Territories were determined by radio-tracking (REVILLA 1998).

We followed the density estimation approach of MCLELLAN (1989), estimating density as a function of the time that each radiotagged animal spent in a fixed area within each population (MCLELLAN 1989). These areas were defined as the minimum convex polygon (MCP) of the locations of all badger captures in Coto del Rey (30 captures, MCP of 7.73 km², maximum span of 4096 m); and of all the winter 1997 trapping stations in the Reserva Biologica (91 stations, MCP of 6.87 km², maximum span 4205 m). Time periods considered for estimation were calendar years. By using this method we assumed that all animals using these areas are known (MCLELLAN 1989). The minimum number of animals living in each territory which overlapped with the areas of density estimation was calculated using sighting information and track censuses. Track censuses were conducted in all territories at least once a year (except in 1994) on previously swept sandy roads (in order to erase old tracks, TRAVAINI 1994). The very high density of roads and fire-breaks at both areas allows the identification of the route of a foraging badger just with its tracks on sand (REVILLA 1998). All radiotagged badgers were continuously tracked during the night preceding the track census, in order to assign their movement routes to the footprint trails (see REVILLA 1998). The results were compared with data obtained using sighting information (both during the night and during sett observations) and tracks around setts (only in the case of young animals). The minimum number of marked plus unmarked individuals was considered as the number of animals using the areas of density estimation. The contribution of every marked animal to the final density was related to the number of days it was known to be present in the area (i.e. only while living in the area). The contribution to the final density of unmarked animals was assumed to be the same as that of other marked individuals from the same territory and period (MACLELLAN 1989). We made two density estimations, one considering all animals (young animals were assumed to add density from the 1st of March), the other considering individuals older than one year (for more details, see MACLELLAN 1989; REVILLA 1998).

Results

Biometry

Males were slightly heavier and larger than females (Table 1), but the results of the ANOVA for weight did not show any significant difference between sexes (F(1,63) = 0.72, P = 0.401), seasons (F(3,63) = 2.10, P = 0.890) or their interaction (F(2,63) = 2.81, P = 0.068). The remaining measurements showed no significant differences between the sexes (MANOVA F(5,56) = 1.49, Wilk's Lambda P = 0.206, Tab. 1). The mean index of sexual dimorphism was 1.038 (SE = 0.008, N = 6), ranging between 1.07 for the weight and 1.02 for ear and tail lengths.

Reproduction

Eight of 11 (73%) registered births were in January, two in December, and one in November. From 1994 to 1997 we monitored reproduction using radiotracking at up to five different territories, totalling 18 year-territory. We confirmed reproduction in ten of them (67%), it was probable in one (6%), and did not occur in four (27%). In the three remaining we could neither confirm nor deny reproduction. Information on litter size was scarce. We registered two foetuses in a pregnant female and three placental scars in another as counts of cubs at birth. A road-casualty female (August 1996) had three unimplanted blastocysts in the uterus, which can be interpreted as a sign of delayed implantation. All females older than two years had bred (N = 19), while only one from five 2-year-old animals had bred. Sixty-five percent of the females older than two years bred in the calendar year of capture (N = 17). All captured males of two years or older had scrotal

Table 1. Mean values, standard deviation (SD), range and number of measured animals (N) for body weight (BW), head-body length (HB), tail length (TL), hilt (HI), ear length (EL), and hindfoot length (HF), of Eurasian badgers, *Meles meles*, from a Spanish Mediterranean population. Lengths are in mm and mass in g.

1	Males				Females			
	mean	range	SD	Ν	mean	range	SD	Ν
BW	7 333	5 850-9 300	921.5	23	6 884	4 800-9 200	1 086.19	40
HB	680.9	582-750	41.10	22	661.2	592-750	39.77	39
TL	160.9	132-180	13.95	22	158.2	114-200	14.86	39
HI	303.0	247-345	24.91	22	287.3	228-315	19.06	38
EL	45.0	34-50	3.39	21	44.2	39-51	2.82	35
HF	104.8	92-115	4.89	22	101.8	88-120	5.75	39

testes (N = 10). Three out of four yearlings also had descended testes (if assumed born in January, two were 14- and one 17-months old). The fourth (14-months old) had abdominal testes. In two young (9- and 11-months old) they were undescended.

Density

In Coto del Rey, the average number of animals inside the trapping area was 10.25 (SE = 1.10, range 9–13), of which, on average, 65% were radio-marked (SE = 0.12, range 44–88%). Average annual density (between 1994 and 1997) was 0.85 individuals/km² (SE = 0.08, range 0.73–1.07) considering all the animals, and of 0.67 individuals/km² (SE = 0.05, range 0.57–0.74), excluding the animals born every year. In the Reserva Biologica, badger density in 1997 was 0.28 and 0.23 individuals/km² (including and excluding yearlings, respectively), of which three (38%) were radio-marked.

Discussion

Biometry

To the best of our knowledge, Eurasian badgers in the Doñana area are smaller than in any other area studied. Average weights were 1.3–1.8 and 1.2–1.7 times larger in the British Isles and central Europe than in Doñana (for males and females, respectively; KRUUK and PARISH 1983; LÜPS and WANDELER 1993; NEAL and CHEESEMAN 1996; ROGERS et al. 1997 a). Doñana badgers were also lighter than badgers from Huesca, north of Spain (LÜPS and WANDELER 1993). Head-body length was 1.1 and 1.21 times larger (respectively for both sexes) in British and German animals than Doñana badgers (LÜPS and WANDE-LER 1993; NEAL and CHEESEMAN 1996).

Smaller animals can be expected in populations where densities are close to the carrying capacity (ROGERS et al.1997 a), but as human-induced mortality is very important in the Doñana area (REVILLA and PALOMARES 1996) this density-dependent size constraint does not seem to be the main reason for the small size. Bergmann's rule predicts that, for a given homeotherm species, individuals will be larger when living at lower mean temperatures; thus, body size of homeotherms is correlated to mean ambient temperature, and therefore to latitude (MARGALEF 1974; MAYR 1956; but see GEIST 1987). Also, animals from populations living in less productive areas are expected to be smaller, as absolute values of maintenance cost and food requirements are reduced (both very important for survival during food stress periods). This has been shown by KRUUK and PARISH (1985) in a badger population where weight of the animals in spring and early summer was lighter after a diminution in the main prey availability (earthworms). The Doñana area is poor for badgers in comparison with areas where earthworms are the staple food. Both nutritional factors and Bergmann's rule seem plausible for explaining body size differences, which in turn fit into the clinal variation of body size across Europe, with smaller animals to the south (LYNCH 1993; NEAL and CHESEEMAN 1996).

There were no significant seasonal variations in body weight. In northern populations, badgers have to spend winters with scarce trophic resources. The negative energetic balance produced by scarcity and low temperatures results in an activity reduction and weight loss (Fowler and RACEY 1988). Winter in non-mountainous Mediterranean areas is rainy and mild with plentiful resources. Badgers in Doñana fed on rabbit kittens during winter (MARTIN et al. 1995) and consequently there is not an adaptative advantage for weight gain in autumn, as in northern populations (NEAL and CHEESEMAN 1996).

Males were not significantly larger than females. In other populations, sexual dimorphism is higher, for example, sexual dimorphism index for body mass was 1.15 in Great Britain and Japan, and 1.16 in Germany and The Netherlands (data from LÜPS and WANDELER 1993; KANEKO et al. 1996; NEAL and CHEESEMAN 1996). One of the hypothesis explaining the sexual dimorphism in mustelids (for a review, see DAYAN and SIMBERLOFF 1996; KING 1989) states that it is a result of sexual competition between males of polygynous species (MOORS 1980; HEDRICK and TEMELES 1989; SHINE 1989). This could suggest that a smaller difference between badger sexes might be related to a greater trend to monogamy (KLEIMAN 1977). In high density populations there is usually only one female breeding per year and territory, but cases where 2 or even 3 females breed are not rare (WOODROFFE and MACDONALD 1993). In Doñana, there was no single case of double or triple births in the same territory (REVILLA 1998; RODRÍGUEZ et al. 1995). This could support the existence of a more strict monogamy in the studied population.

Reproduction

Our results are in accordance with the general trend towards earlier birth dates in the more southerly European populations (NEAL and CHEESEMAN 1996). In Doñana we estimated the average birth date to be within the first week of January whereas in southwest France it is 31 January; in southwest England 7 February; early March in Scotland, Germany, and Sweden and, late March in Russia (NEAL and CHEESEMAN 1996). We did not detect multiple births within a territory and reproduction occurred or most probably occurred in only 73% of controlled territories, which means that in 27% of territories there was no cub recruitment. Of adult females captured (older than two years), 65% bred the year of capture. This is much higher than the 20–40% found by RogERS et al. (1997 a) in a high density population; but similar to the 73% of breeding females 5 years or older (which are the group dominants, RogERS et al. 1997 a). Despite the small sample size and potentially large range of error in our estimations, the number of cubs and the year of the first reproduction were similar to other studied populations (AHNLUND 1980; CANIVENC 1966; PAGE et al. 1994)

Density

It is assumed that density in the Reserva Biologica is the lowest ever recorded. This area, composed of stabilised dunes and pine plantations, is adjacent to an area dominated by Mediterranean scrubland where RODRÍGUEZ et al. (1995) recorded badgers at 0.5 individuals/km². Based on rabbit abundance (MARTIN et al. 1995; RODRÍGUEZ et al. 1995) our density should be expected to be lower than that calculated by RODRÍGUEZ et al. (1995) because rabbits are more abundant in Mediterranean scrubland (PALOMARES et

al. 1996). In Coto del Rey, badger density was 3.5 times larger than in the Reserva Biologica, and rabbit densities were up to 25 times higher (REVILLA 1998). However, the Reserva Biologica population does not rely on rabbits but on a diversity of food resources, and thus density should be related to the abundance and spatial distribution of these resources, not only to rabbits (KRUUK 1978; MACDONALD 1983; WOODROFFE and MACDONALD 1993). Densities in these Mediterranean populations are 5 to 125 times smaller than those in Eurasian temperate ecosystems (WOODROFFE and MACDONALD 1993), where earthworms form the main part of the diet (they represent only secondary prey in Mediterranean areas; IBAÑEZ and IBAÑEZ 1977; KRUUK, 1989; MARTÍN et al. 1995; PIGOZZI 1988; RODRÍGUEZ and DELIBES 1992; REVILLA 1998). The wide variation in badger densities can be seen as a gradient of functional responses to the diverse carrying capacity of landscapes, with the highest found at Eurosiberian temperate areas, as stated by Rogers et al. (1997b). Carrying capacity follows the availability of earthworms through Europe, fluctuating according to differences in annual rainfall and on any other main resource, such as rabbits. Variations in this and other population parameters can be expected for many other areas of the species distribution (boreal forests, mountainous areas, arid areas, and steppes of Asia) where earthworms are not the staple resource (Roper and Mickevicius 1995).

Eurasian badgers living in this Mediterranean area are different from central European populations and thus their management and conservation needs should be considered separately. To determine the right management and conservation measures, further research is necessary on Mediterranean populations focussing on taxonomic status (GRIF-FITHS and THOMAS 1997), abundance and distribution (BLANCO and GONZÁLEZ 1992) and behavioural ecology (REVILLA 1998).

Acknowledgements

The authors would like to acknowledge J. AYALA J. CALZADA, J. M. FEDRIANI, P. FERRERAS, R. LAFFITE, and R. MARTÍN, for trapping some of the animals. CLAIRE SEYMOUR and GUYONNE JANSS greatly improved the English. S. T. WIEGAN kindly reviewed and translated the Zusammenfassung. ER had a predoctoral grant from the Spanish Ministry of Education and Culture. This study was partially financed by the Spanish CAICYT and DGICYT (project numbers 944, PB87-0405, PB90-1018, PB94-0480, and PB97-1163) and sponsored by Rover España.

Zusammenfassung

Physische und demographische Parameter des Eurasischen Dachses (Meles meles L.) im mediterranen Spanien

Es werden Informationen über Biometrie, Reproduktion und Populationsdichten einer Population von Dachsen dem mediterranen Spanien vorgestellt. Die Dachse waren im Vergleich zu anderen untersuchten Populationen kleiner, leichter und sexuell weniger dimorph. Es konnten keine signifikanten jahreszeitlich bedingten Gewichtsunterschiede festgestellt werden. Die meisten Geburten wurden im Januar beobachtet; in 67% der kontrollierten Territorien trat ein Wurf pro Jahr auf und alle Weibchen über 2 Jahre hatten Junge (wobei 65% der Weibchen im Jahr des Fangs setzten). Die Populationsdichte schwankte zwischen 0,23 und 0,67 Individuen/km², für die geringsten und am höchsten produktiven Zonen des Untersuchungsgebietes. Diese Werte sind etwa 5 bis 125fach kleiner als Dichten von Dachspopulationen in Ökosystemen gemäßigten Klimas. Die biometrischen und reproduktiven Parameter fügen sich in eine europäische Kline ein. Die geringen Dichten können als funktionelle Antwort auf die unterschiedlichen trophischen Ressourcen mediterraner Populationen erklärt werden. Ähnlich geringe Dichten sind auch für viele andere Dachspopulationen zu erwarten, bei denen Regenwürmer keine Hauptnahrungsquelle sind.

References

- AHNLUND, H. (1980): Sexual maturity and breeding season of the badger, *Meles meles*, in Sweden. J. Zool. (London) **190**, 77–95.
- BLANCO, J. C.; GONZÁLEZ, J. L. (Eds.) (1992): Libro Rojo de los vertebrados de España. Madrid: ICO-NA.
- CANIVENC, R. (1966): A study of progestation in the European badger (*Meles meles* L.). Symp. Zool. Soc. Lond. 15, 15–26.
- CASTRI, di F.; MOONEY, H. A. (Eds.) (1973): Mediterranean type ecosytems: origin and structure. Berlin: Springer-Verlag.
- DAYAN, T.; SIMBERLOFF, D. (1996): Patterns of size separation in carnivore communities. In: Carnivore Behavior, Ecology, and Evolution, Vol. 2. Ed. by J. L. GITTLEMAN. Ithaca: Cornell Univ. Press. Pp. 243–266.
- DELIBES, M. (1975): Some characteristic features of predation in the Iberian Mediterranian ecosystem. In: Proceedings of the XII International Union of Game Biologists. Lisboa: Direcçao Geral dos Recursos Forestais. Servicio de Inspecçao da Caça e Pesca. Pp. 31–36.
- FEDRIANI, J. M.; FERRERAS, P.; DELIBES, M. (1998): Dietary response of the Eurasian badger, *Meles meles*, to a decline of its main prey in the Doñana National Park. J. Zool. (London) **245**, 214–218.
- Fowler, P. A.; RACEY, P. A. (1988): Overwintering strategies of the badger, *Meles meles*, at 57 °N. J. Zool. (London) **214**, 635–651.
- GEIST, V. (1987): Bergmann's rule is invalid. Can. J. Zool. 65, 1035-1038.
- GRIFFITHS, H. I.; THOMAS, D. H. (1997): The conservation and management of the European badger (*Meles meles*). Strasbourg: Council of Europe.
- HEDRICK, A. V.; TEMELES, E. J. (1989): The evolution of sexual dimorphism in animals: hypotheses and tests. Trends Ecol. Evol. 4, 136–138.
- IBAÑEZ, C.; IBAÑEZ, J. I. (1977): Alimentación del tejón en el Rasillo de Cameros (Logroño, España). In: Actas I Reunión Iberoamer. Zool. Vert., La Rábida, Spain. Sevilla: Estación Biológica de Doñana. Pp. 517–527.
- KANEKO, Y.; MARUYAMA, N.; KANZAKI, N. (1996): Growth and seasonal changes in body weight and size of japanese badger in Hinodecho, suburb of Tokyo. J. Wildl. Res. 1, 42–46.
- KING, C. M. (1989): The advantages and disadvantages of small size to weasels, *Mystela*, species. In: Carnivore Behavior, Ecology, and Evolution, Vol. 1 Ed. by J. L. GITTLEMAN. London: Chapman and Hall. Pp. 302–334.
- KLEIMAN, D. G. (1977): Monogamy in mammals. Quart. Rev. Biol. 52, 39-69.
- KLEVEZAL, G. A. (1996): Recording structures of mammals. Determination of age and reconstruction of life history. Rotterdam: A. A. Balkema.
- KRUUK, H. (1978): Spatial organization and territorial behaviour of the European badger Meles meles. J. Zool. (London) 184, 1–19.
- KRUUK, H. (1989): The social badger. Ecology and behaviour of a group-living Carnivore (*Meles meles*). Oxford: Oxford Univ. Press.
- KRUUK, H.; PARISH, T. (1983): Seasonal and local differences in the weight of European badgers (*Meles meles L.*) in relation to food supply. Z. Säugetierkunde 48, 45–50.
- KRUUK, H.; PARISH, T. (1985): Food, food availability and weight of badgers (*Meles meles*) in relation to agricultural changes. J. Appl. Ecol. 22, 705–715.
- LONG, C. A.; KILLINGLEY, C. A. (1983): The Badgers of the World. Springfield, Illinois: Charles C. Thomas.
- LÜPS, P.; WANDELER, A. I. (1993): *Meles meles* (Linnaeus, 1758) Dachs. In: Handbuch der Säugetiere Europas. Raubsäuger, Teil 2. Ed. by M. STUBBE and F. KRAPP. Wiesbaden: AULA-Verlag. Pp. 856–906.
- LYNCH, J. (1993): Craniometric variation in selected Mustelidae. PhD thesis. Nat. Univ. of Ireland, Dublin, Ireland.
- MACDONALD, D. W. (1983): The ecology of carnivore social behaviour. Nature 301, 379-384.
- MARGALEF, R. (1974): Ecologia. Barcelona: Ediciones Omega.
- MARTÍN, R.; RODRÍGUEZ, A.; DELIBES, M. (1995): Local feeding specialization by badgers (*Meles meles*) in a mediterranean environment. Oecologia **101**, 45–50.
- MAYR, E. (1956): Geographical gradients and climatic adaptation. Evolution 10, 105-108.
- MCLELLAN, B. N. (1989): Dynamics of a grizzly bear population during a period of industrial resource extraction. I. Density and age-sex composition. Can J. Zool. **67**, 1856–1860.

- Moors, P. J. (1980): Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. Oikos **34**, 147–158.
- NEAL, E.; CHEESEMAN, C. (1996): Badgers. London: T and A D Poyser.
- PAGE, R. J. C.; ROSS, J.; LANGTON, S. D. (1994): Seasonality of reproduction in the European badger Meles meles in south-west England. J. Zool. (London) 233, 69–91.
- PALOMARES, F.; CALZADA, J.; REVILLA, E. (1996): El manejo del hábitat y la abundancia de conejos: diferencias entre dos área potencialmente idénticas. Revista Florestal 9, 201–210.
- PIGOZZI, G. (1988): Diet of the European badger (*Meles meles L.*) in the Maremma Natural Park, Central Italy. Mammal Rev. 18, 73–75.
- REVILLA, E. (1998): Organización social del tejón en Doñana. PhD thesis, Univ. of León, Spain.
- REVILLA, E.; PALOMARES, F. (1996): Los furtivos matan a la mitad de los tejones marcados en Doñana. Quercus 131, 46.
- RODRÍGUEZ, A.; DELIBES, M. (1992): Food habits of badgers (*Meles meles*) in an arid habitat. J. Zool. (London) **227**, 347–350.
- RODRÍGUEZ, A.; MARTÍN, R.; DELIBES, M. (1995): Space use and activity in a mediterranean population of badgers (*Meles meles*). Acta Theriol. **41**, 59–72.
- ROGERS, L. M.; CHEESEMAN, C. L.; LANGTON, S. (1997a): Body weight as indication of density-dependent population regulation in badgers (*Meles meles*) at Woodchester Park, Gloucestershire. J. Zool. (London) 242, 597–604.
- ROGERS, L. M.; CHEESEMAN, C. L.; MALLINSON, P. J.; CLIFTON-HADLEY, R. (1997 b): The demography of a high-density badgers (*Meles meles*) population in the west of England. J. Zool. (London) 242, 705– 728.
- ROPER, T. J.; MICKEVICIUS, E. (1995): Badger *Meles meles* diet: a review of literature from the former Soviet Union. Mammal Rev. 25, 117–129.
- SHINE, R. (1989): Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quart. Rev. Biol. 64, 419–461.
- TRAVAINI, A. (1994): Demografía de la población de zorros (Vulpes vulpes) del Parque Nacional de Doñana. PhD thesis, Univ. Autónoma of Madrid, Spain.
- TRAVAINI, A.; DELIBES, M. (1995): Weight and external measurements of red foxes (*Vulpes vulpes*) from SW Spain. Z. Säugetierkunde 60, 121–123.
- WOODROFFE, R. (1995): Body condition affects implantation date in the European badger, *Meles meles*. J. Zool. (London) 236, 183–188.
- WOODROFFE, R.; MACDONALD, D. W. (1993): Badger sociality-models of spatial grouping. Symp. zool. Soc. Lond. 65, 145–169.
- WOODROFFE, R.; MACDONALD, D. W. (1995 a): Cost of breeding status in the European badger, Meles meles. J. Zool. (London) 235, 237–245.
- WOODROFFE, R.; MACDONALD, D. W. (1995 b): Female/female competition in European badgers Meles meles: effects on breeding success. J. Anim. Ecol. 64, 12–20.
- WOODROFFE, R.; MACDONALD, D. W.; CHEESEMAN, C. L. (1997): Endocrine correlates of contrasting male mating strategies in the European badger (*Meles meles*). J. Zool. (London) 241, 291–300.
- ZAPATA, S. C.; GARCÍA PEREA, R.; BELTRÁN, J. F.; FERRERAS, P.; DELIBES, M. (1997): Age determination of Iberian lynx (*Lynx pardinus*) using canine radiograph and cementum annuli enumeration. Z. Säugetierkunde 62, 119–123.
- ZAPATA, S. C.; TRAVAINI, A.; DELIBES, M. (1995): Comparación entre varias técnicas de estimación de la edad en zorros, *Vulpes vulpes*, de Doñana (Sur de la Peninsula Ibérica). Doñana, Acta Vertebrata 22, 29–50.
- ZAR, J. H. (1996): Biostatistical analysis. Upper Saddle River: Simon and Schuster.
- Authors' addresses: ELOY REVILLA, MIGUEL DELIBES, and FRANCISCO PALOMARES, Department of Applied Biology, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Avenida de Maria Luisa s/n, E-41013 Sevilla, Spain; ALEJANDRO TRA-VAINI, Centro de Investigaciones de Puerto Deseado, Almirante Brown y Colón s/n, Puerto Deseado, Santa Cruz 9050, Argentina